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## Thomas Conrad Porter

BY N. L. BRITTON

(WITH PORTRAIT)

Professor Porter died suddenly at his home in Easton, Pa., on the evening of April 27, 1901. He was born at Alexandria, Pa., January 22, 1822, and was thus over seventy-nine years of age. His end was painless; he was writing a letter when the stroke came that ended his long and valuable life.

His boyhood was spent at Alexandria and at the Harrisburg Academy, Harrisburg, Pa. He was graduated from Lafayette College in 1840, and received the degree of Master of Arts from that institution in 1843, after studying theology for a time at Princeton Seminary. He was pastor of the Second Reformed Church at Reading, Pa., from 1848 in 1849 and in 1848 was elected to the professorship of natural sciences in Marshall College, Mercersburg, Pa., and subsequently upon the union of that institution with Franklin College forming the present Franklin and Marshall College, he occupied the same chair until 1866, in which year he accepted a call to the Jesse Chamberlin professorship of Botany in Lafayette College, Easton, Pa., which he held until January, 1897, teaching also zoölogy and general geology, thus having served the institution for 30 years. At this time he retired from active professional duties, but retained a connection with Lafayette as Emeritus Professor, Dean of Pardee Hall, and Curator of the Botanical Collections, until his death.

The degree of Doctor of Divinity was conferred upon him by Rutgers College in 1865, and that of Doctor of Letters by Franklin and Marshall College in 1880. As early as 1840 he began the collecting and critical study of the plants of his native State, and this work was continued almost without interruption to the end of his life. He has thus brought together one of the most complete and representative State herbaria yet formed, which Lafayette College will doubtless prize as one of its choicest scientific assets. He was in correspondence with nearly everybody interested in native plants in Pennsylvania during his time, and in personal coöperation with most of his correspondents, stimulating interest in natural objects and natural phenomena in a most valuable way, as he was always willing to supply freely any information at his command. He personally explored, at one time or another, nearly all portions of the State; he was a profuse collector, and a liberal distributer, hence nearly all the permanent herbaria of the country have been enriched directly or indirectly by specimens prepared and named by him, and many have found their way to Europe. He has long had in preparation a volume recording the local distribution of the flora of Pennsylvania. This has been posted up with the numerous new discoveries made by himself and others, and has for several years been essentially ready for publication, but Dr. Porter's ambition was always to make it more and more complete and consequently the more valuable; so much interested was he in this research that he has provided for its ultimate publication in his will.

In 1846 he explored northern Georgia in company with the distinguished naturalist, Dr. Joseph LeConte, of Philadelphia, and brought back a noteworthy collection of botanical specimens, a number of which proved to represent species new to science; this became the nucleus of his general herbarium, which was continuously increased by his personal collections in various parts of the United States and numerous exchanges with American and European botanists, until it became one of the important accumulations of specimens in the country. It was, most unfortunately, somewhat injured by the incendiary fire which seriously damaged the Pardee Hall of Lafayette College in 1897, but it still remains a notable collection; this herbarium contains the records of his

important pioneer work in the study of the Rocky Mountain flora in connection with the U. S. Geol. and Geog. Survey of the Territories in 1869–74 under Dr. F. V. Hayden, and these specimens are historically important inasmuch as comparatively few duplicates were obtained. Dr. Porter visited Wyoming and Colorado while engaged in this study in company with his friend Dr. Joseph Leidy, of Philadelphia.

Dr. Porter's generous coöperation in the work which it has fallen to the writer to direct has been of the greatest assistance. I first made his personal acquaintance in 1878, when beginning the bringing together of materials for the Preliminary Catalogue of New Jersey Plants, published by the Geological Survey of that State in 1880. Learning that this work was in progress he promptly offered to put at my disposal all the notes and specimens accumulated by him during many years of observation of the flora of the Delaware River valley and these served to notably improve the records of local distribution and habitat of the plants of the State. During the ten years from 1880 to 1890 while the further botanical exploration of the State was going forward, preparatory to the publication of the Catalogue of Plants, in the final reports of the State Geologist the late Geo. H. Cook, Dr. Porter and I were in constant communication, and he joined me in many collecting trips besides making numerous individual visits to various parts of the State in the interests of this work.

In 1890, when I commenced writing "Illustrated Flora" this coöperation was enthusiastically continued and many of the new facts brought out in that book were obtained from studies with him in the field or in his herbarium; his advice and aid were also freely given during the work for the establishment of the New York Botanical Garden, and he supplied up to the time when failing health restricted his activity many valuable specimens for the collections of that institution. Dr. Porter also contributed much to the building of the botanical collections of the Academy of Natural Sciences of Philadelphia. During the life of the late Dr. Asa Gray he was in constant communication with him relative to the progress of the "Synoptical Flora of North America," and his herbarium was greatly enriched by contributions of Dr. Porter's notes and specimens; his coöperation with Dr. Torrey is also evi-

denced by the numerous specimens preserved in the herbarium of Columbia University.

Enough has been said in the preceding paragraphs to indicate the bent of Dr. Porter's botanical activity. He was primarily a coöperator in the work of other students; his tendency was to help others, and this almost over-generous nature militated against his own original work becoming as prominent as its importance warranted. His very sociable personality further illustrates this tendency; he disliked to be alone and his best observations were always made in the company of others. He never missed an opportunity of participating in the field excursions of the Torrey Club or of the Philadelphia Botanical Club, both of which organizations claimed him as an honored and active member, and whose formal meetings he occasionally attended. He was a fluent and forceful speaker and his addresses received the closest attention.

Dr. Porter's knowledge of plant habitats and environment drawn from many years of close observation was remarkable. Over and over again I have known him to remark that a locality visited for the first time, was a "likely place" for certain species to grow and the chances were all in favor of the plant being found within the next few minutes. The terminology and philosophic methods of modern ecology came in too late in his life for him to appreciate their true value, but his knowledge of the facts on which that science is based was wonderfully broad.

In recognition of Dr. Porter's services to botanical science the genera *Porterella* in the Lobeliaceae and *Porteranthus* in the Rosaceae, have been dedicated to him; species or subspecies have also been named in his honor in the genera *Gymnolomia*, *Aster*, *Viola*, *Panicum*, *Muhlenbergia*, *Calamagrostis*, *Bromus*, *Eriogonum*, *Ranunculus*, *Crataegus*, *Senecio*, *Desmatodon*, *Orthotrichum*, and others. His published botanical papers include over fifty titles.

He described as new to science species or subspecies in the genera *Aster*, *Solidago*, *Carex*, *Avena*, *Melica*, *Calochortus*, *Habenaria*, *Boehmeria*, *Anemone*, *Clematis*, *Arabis*, *Fragaria*, *Geum*, *Prunus*, *Trifolium*, *Astragalus*, *Gerardia*, *Eupatorium*, *Lacinaria*, *Aplopappus*, *Erigeron*, and *Cyperus*.

While botany is the science in which his life work will most permanently be recorded, it was by no means the only study in

which he was interested. Reference has already been made to his theological training, and his interest in the subject was continued throughout his life, he frequently being called on to preach after his early pastoral duties had been exchanged for those of his professorship. Geology and zoölogy each claimed a share in his attention, and in these sciences as in botany he contributed many new facts to students and to investigators of his acquaintance, besides carrying on the pedagogic work in them at Lafayette College during a series of years. Literature was not neglected; it indeed was one of his favorite pursuits, and its enjoyment was shared by his wife, who died only a few weeks before him. His greatest prominence in literary fields came from his contention in 1858, immediately after the first publication of Professor Longfellow's poem "Hiawatha," that its inspiration was derived from the ancient Finnish epic, the Calevala. Dr. Porter publicly maintained that the New England poet had "transferred the entire form, spirit and many of the striking incidents of the old Finnic epic to the North American Indians. The resemblance is so close that it cannot be accidental, and that without the slightest acknowledgment of the source of his inspiration." This statement provoked much controversy, but Dr. John M. Crawford maintains that it is true.

# The Anatomy of Phoradendron villosum Nutt.

By W. A. Cannon

(With Plates 27, 28)

The California species of the American mistletoe (*P. villosum*), in the vicinity of Stanford University, is found on several kinds of evergreen and deciduous trees, among which are the following: Common locust (*Robinia pseudacacia*), Lombardy poplar (*Populus nigra*), species of willow, and the Roble, Douglas, Encina, and Kellogg oaks (*Quercus lobata, Q. Douglasii, Q. agrifolia* and *Q. Kelloggii*) and it has been reported from Chico, California, as occurring on the cultivated peach. The parasite is abundant on the Roble oak, and since the latter is common in the vicinity of the university, it was chosen to study as the host.

The present paper deals merely with the anatomy of the mistletoe, but it is intended that it shall be followed as soon as convenient by a contribution from the Botanical Laboratory on the biology of the plant.

The material was collected mainly in the spring and early summer of 1899. It was killed with alcoholic corrosive sublimate, and all of the sections were cut by hand.

This study was carried on under the direction of Dr. G. J. Peirce, to whom I take pleasure in expressing my gratitude for his great helpfulness in this, and in other work.

## 1. The Leaf

The leaves of the mistletoe are borne in alternating pairs on stout stems, which arise from the host at varying angles in respect to the horizon, and consequently in reacting to the light, the leaves assume a more or less vertical position and become bent in petiole and blade. They are relatively thick, of a yellowish-green color, and are markedly brittle. There is a regular gradation in the size of the leaves throughout the younger portion of the plant, so that it is impossible to assign most of them to a definite season's growth. The mature ones measure 3.25–4 cm. in length by 2.5 cm. in

breadth. The youngest leaves which may be seen in early spring measure .3 by .75 cm., while the next older ones are 1–1.25 by 1.75–2.25 cm. There is a like difference in measurement between the second and third sets of leaves, and also, the differences in area of the first two seasons' leaves are generally paralleled by a difference in thickness. The leaves do not increase in thickness after the second season.

The tips of the youngest leaves are projected beyond the growing point of the stem, and their dorsal surfaces are closely pressed together. The surfaces thus in contact are inaccessible to the light and are colorless, while exposed surfaces take on the color characteristic of the plant. A cross section of such a leaf shows that it has a well-defined epidermis, and a mesophyll composed of similar cubical cells with small intercellular spaces. The cuticle of the dorsal surface is noticeably thinner than that of the ventral (Fig. 3) and this, like the coloration, may be in some manner associated with the length of exposure to the light. A relatively large number of epidermal cells on both sides of the leaves are prolonged into long trichomes with bulbous bases, and both trichomes and epidermal cells are well filled with finely granular protoplasm and and are provided with large nuclei. The cells of the mesophyll, in the second season, become elongated and palisade-like, and it is to the lengthening of the mesophyll cells in a direction at right angles to the surface of the leaf, that the increase in thickness, spoken of above, is due. (Fig. 4.) In this regard *P. villosum* recalls *Viscum album.* * The increase in thickness from the first to the second season is as the ratio 1 : 2. † The measurements are .4 mm. for the first, and .79 mm. for the following season. As the leaves mature the cell walls become pitted, a large number of them are found with crystal aggregates (calcium oxalate), and prominent intercellular spaces are developed. Another characteristic of the old leaf is the kind and position of the stomata. The stomata, which are found on both sides of the leaves, are of the xerophytic type described and figured by Schimper, ‡ and while they are con-

* Marktanner-Turneretscher, Sitzungs. d. k. Akad. d. Wissen. Math.-Natur. Classe, 91 : 5 Heft, May, 1885.

† Warming, Pflanzengeographie, 302.

‡ Schimper, Pflanzengeographie, 7.

siderably sunken beneath the surface they are less so than those of the stem. In comparing the stomates of the mistletoe with those of the oak in regard to size and number, it is found that those of the former are about twice as large (Fig. 2) and only approximately half as many to a given area as those of the latter. The number of stomates per square millimeter on each surface of the mistletoe leaf is about 40, while on the oak, where they occur on one side only, there are about 80.

The conductive system of the leaf is poorly developed and the tracheids at the ends of the leaf traces are not swollen as in *Loranthus*, and to some extent in *Viscum*.* No water reservoirs, such as are described by Marktanner-Turneretscher for *Viscum*, the presence of which is denied by Solereder, † are to be found in *P. villosum*.

The color given to the mistletoe by the cuticle, which was spoken of above, has led to a supposition that there is a peculiar quality of chlorophyll in the plant that is in some manner associated with its parasitic habit. This is not at all the case. The external color of the plant is entirely due to the coloration of the cuticle, and the chlorophyll, as far as I could determine, was quite normal. I tried to dissolve out the coloring matter from the cuticle by using the common solvents and thus learn its nature, but in this I was quite unsuccessful.

The leaf of the mistletoe is mechanically very weak. This is partly due to the poor development of supporting tissue, but chiefly to the prominent intercellular spaces. If a leaf is broken in two, and sections are cut at right angles to the fracture, it will be seen that the line of fracture passes between the cells, or that, in other words, it coincides with the intercellular spaces. It is likely here as in the stem that perhaps the main element of strength lies in the unusual development of the outer epidermal wall, the cuticle. This will be spoken of again later in this paper.

### 2. THE STEM

A cross section of a young stem shows a wood cylinder made up as usual of conductive tissue, medullary rays, wood paren-

* Marktanner-Turneretscher, l. c.

† Solereder, Anatomie der Dicotyledonen.

chyma, and pith, and also, a cortex with a well-defined epidermis. The young epidermal cells are cubical in form, but as the stem increases in diameter they and the underlying cells for some distance become much flattened. The lateral and internal walls of the epidermal cells bear numerous pits (Fig. 6). Some of the outer cells project as trichomes and some are modified to form stomata which are deeply sunken in the older parts of the stem (Fig. 5), and are of the xerophytic type, the stomata of which are placed longitudinally.

The cortex of the young stem is composed of thin-walled cells with intercellular spaces. As the stem becomes larger the walls of these cells increase in thickness until in the older parts they are relatively very heavy. They, at the same time, develop numerous pits. The intercellular spaces also in the older stem take on the characters which we have seen to be so pronounced in the leaves. Groups of grit cells and cells bearing calcium oxalate crystals are noticeable characteristics of the old stems.

Within the cortex of the young stem is a ring of several fibrovascular bundles, of the open collateral type, separated by medullary rays. A group of hard bast fibers, which are derived from the pro-phloëm, is found inside of the pericycle exterior to each bundle. Subsequently no hard bast is formed in the stem. Also, on the inside of each bundle opposite the group of hard bast fibers, is another group of hard bast-like fibers. These two groups of sclerenchymatous tissue can be recognized in the old stems although in these they occupy but a small proportion of the entire area. The first definitive wood elements to be recognized are the ringed tracheids, and later reticulated tracheids, which with the growth of the stem become changed into tracheid-like ducts by the reabsorption of the division walls. But the form of the tracheids of which the ducts are composed is clearly recognizable. Associated with the ducts are elongated cells, which become thick-walled and form the wood fibers of the xylem. When these fibers are young they present much the appearance of slime canals. The contents of the fibers give the sugar reaction with Fehling's solution, and in the younger ones, the walls are cellulose. In all old fibers, however, these walls are lignified. If the fibers function as slime canals at any time they probably cease

to do so when the change in composition of the walls takes place. It should be said that the slime canals in *Arceuthobium* are of quite different character, and also that they entirely, or for the most part, occur in the cortex of the stem. Short cells with heavy, pitted walls form the wood parenchyma and constitute a relatively large proportion of the wood elements. Attention may be called here to the structure of the wood cylinder as regards mechanical strength although that will be considered more fully below. The element of strength, the relatively large number of fibers, of the oak stem, is seen to be wanting in the mistletoe, and those kinds of cells which do not contribute primarily to the strength of the stem, the wood parenchyma, and which are present in a small amount in the oak, are again the most abundant in the mistletoe.

The pith of the young stem is composed of cells which are quite like those of the medullary rays and of the cortex, but in the old stem they become heavily walled, and because of the presence of pits, have a peculiarly ragged appearance in cross section. And it should be said that perhaps the most striking character of the stem is the presence in the pith and cortex, mainly in the pith, of heavy walls and of correspondingly deep pits.

The stem of this mistletoe, like the leaf, is mechanically very weak. A comparatively small amount of force is needed to snap it in two, and this weakness is in a measure independent of the size of the stem. The reason for the brittleness can doubtless be found in its structure. Among the factors that make for this condition may be counted the great number of crystal-bearing cells, the large number of grit cells, the presence of prominent intercellular spaces, and of deep pits in the walls of the parenchymatous cells. And to these may be added also the absence of secondary bast fibers, the small number of wood fibers present, the peculiar tracheid character of the wood ducts, and the relatively large amount of xylem parenchyma. The greatest single source of strength is probably the outer wall, the cuticle, of the periderm. If the cuticle is carefully removed for a short distance, say 5 cm., from a portion of the stem, the end of which is firmly secured, and weights are placed on the free end, the stem will bend and finally break in the region from which this has been removed. The ininfluence of the weights will hardly be observed in other parts of

the stem, and will scarcely affect a similar one from which the cuticle has not been removed. Further, if the fracture of the mistletoe stem be compared with that of an oak a difference characteristic of the structure of the two may be seen. The mistletoe stem breaks straight across with no tendency to split, while the oak breaks irregularly and splits at frequent intervals.

### 3. THE HAUSTORIA

The mistletoe is attached to its host by haustoria, which in structure and in function show evident differentiation. The young haustoria ramify in all directions in the cortex of the host and they may even quite encircle the central cylinder.* From these others turn sharply toward the center of the host branch, and become partly enclosed by it. These latter are the so-called sinkers of the parasite. Upon a considerable increase in diameter of the cortical haustoria, the cells of the cortex of the host, which are outside of the haustoria, gradually loose their contents and die and the haustoria are in this manner exposed to the air. They undergo considerable change in structure in the meantime. There are thus three easily distinguishable sorts of haustoria, which, for convenience I shall refer to as cortical haustoria, sinkers, and aërial haustoria.

The youngest cortical haustoria are composed throughout of thin-walled parenchyma. All of the cells are densely filled with a coarsely granular material which gives a starch reaction. While the cells of the interior of the haustoria are pretty much alike, those corresponding to the epidermis are somewhat differentiated. In some portions of the haustoria the outer cells appear much like typical epidermal cells, and in others, at the growing parts, they are much elongated and are papilla-like (Fig. 9). The latter recall those in the region of the young haustoria in the dodder,† as well as the epithelial cells in the scutellum of grasses, ‡ and they appear to have a function analogous to both. The elongated cells of the mistletoe haustoria secrete a solvent that is capable of digesting

* In *Viscum* the haustoria do not surround the stem of the host. Kerner and Oliver, Natural History of Plants, 208.

† Peirce, Annals of Botany, Sept., 1893.

‡ Lermer and Holzner, Beiträge zur Kenntniss der Gerste. Munich, 1888.

most, although it would seem not all, of the cortical tissues of the host. These cells contain finely granular protoplasm, and nuclei which are larger than those in the interior of the haustoria. The host cells which are adjacent to those of the haustoria are rich in food material and they stimulate to great activity the epithelial haustorial cells just described. The adjacent host cells show evident signs of breaking down, and usually a small space intervenes between them and those of the parasite. It has already been stated that the epithelial cells appear to be unable to dissolve certain of the host tissues; these are the sclerenchyma of the oak. The form and size of the digestive cells vary with the changes in structure of the host cells. The former are relatively long when the host tissues furnish them with an abundance of food, but they become short and cubical when the adjacent host cells are poor in food as, for instance, when they are near the surface of the host stem. In the latter case the epithelial cells insensibly merge into the more typical epidermal cells. Not only is the shape and size of the epithelial cells dependent on the character of the adjacent host tissue, but it will soon appear that the ramifications of the haustoria through the cortex are also dependent on the same factor, because the epithelial cells make clear the way for the advancing haustoria.

The tissues within the epidermis of the cortical haustoria become differentiated early into a central conductive system and a surrounding cortex. The cortex is composed of thin-walled cells with intercellular spaces. These cells, like those of the cortical haustoria in general, except the conductive system and the epithelium, are well filled with coarse grains of starch. Grit cells are present in the cortex, but it is not possible in every case to say whether they originated in the cortex of the host or that of the parasite. Sections of young cortical haustoria frequently show numerous masses of fully-developed grit cells in the midst of young and thin-walled parenchyma, and such grit cells have been surrounded, but not digested by the epithelial haustoria cells and come finally to lie wholly within the tissues of the parasite.

The conductive tissues of the cortical haustoria are developed late and possess elements which resemble analogous portions of the stem. Ducts appear in what may be termed the central cylin-

der, and cambiform cells occur between the cylinder and the cortex. The cortical haustoria do not begin secondary growth until they cease to function as food absorbers and serve the parasite as food conductors, and to some extent as food reservoirs. With this change in function appears a change in structure, and the cortical haustoria pass over into the aërial haustoria which will be spoken of later.

Before examining the structure of the haustoria of the mistletoe further it will be best to briefly glance at the main characters of the structure of the host branch (Roble oak, *Quercus lobata*) on which the parasite grows.

The oak branch is made up of a central cylinder surrounded by a cortex. The cylinder is composed of a relatively large number of fibers, of a small amount of wood parenchyma, of radiating medullary rays, and intermingled with other wood elements, especially in spring wood, are also large and small tracheae, or ducts. The wood parenchyma and medullary rays are living cells and are well supplied with food. The ducts are lifeless and serve for the transport of food materials in solution, which have been taken by the roots of the host plant. Most of the prosenchyma cells have scarcely any lumen and are lifeless, and it may be said in passing that the oak owes its strength to the relatively great amount of wood fibers of the wood cylinder. As indicated above, the wood fibers of the mistletoe are present in relatively small numbers, and in this connection a comparison of the two sorts of stems is of interest.

The cortex of the oak is made up of small parenchymatous cells which are compactly set together, of several concentric rings of sclerenchymatous fibers arranged in groups, and of scattered grit cells. Instead of an epidermis, as in the mistletoe, the oak has a few layers of cork which are derived from a superficially placed cork cambium. A meristematic zone of cells, the cambium, separates the cortex from the central cylinder. The outer fibers are lignified, but the inner are not uniformly so. The grit cells are also lignified. Of these tissues, the parenchyma and the meristematic region are richly supplied with food, and it is among the cells of these that the cortical haustoria of the parasite ramify.

Taking up now the growth of the haustoria in the cortex of

the host and their later development into sinkers, it will be seen that the haustoria seek only those cells which contain food; they are chemotactic, and this may be called the positive element in the growth of the haustoria. The negative element is found in those host cells which are either poor in food, or furnish mechanical resistance to the progress of the haustoria, or both. The cells toward the periphery of the branch would represent the first, and the grit cells and fibers the second conditions. How masses of grit cells may affect the growth of the haustoria has already been touched upon. It was found, however, that owing to the characteristic form of these cells the haustoria could envelop them with their own tissues and flow past them, the course of growth not being changed by their presence. The case is somewhat different in regard to the fibers in the cortex of the oak, and they are an important factor in directing the growth of the cortical haustoria as well as those haustoria which penetrate into the xylem of the host. The position and number of sinkers are to a great degree, and perhaps wholly, controlled by the permeability of the inner ring of fibers to the haustoria. From the outer cortical cells of the host the haustoria grope between masses of fibers which compose the outer ring of sclerenchyma to the parenchyma within (Fig. 13), and in a similar manner through the second and each ring of fibers and parenchyma in succession until the inner ring is reached, and the haustoria pass between the gaps in this ring and penetrate the bast and become transformed into sinkers. In every instance the haustoria pass from an area poorer in food to one richer, and they are led in this manner to a position opposite the medullary rays so that with an increase in diameter of the host stem they are in position to supplant them. Such in brief is the origin of the sinkers.

A young sinker is in no respect different from any other part of a cortical haustorium. It originates on that part toward the wood cylinder and, as has just been stated, becomes a sinker by penetrating between some gap in the inner fiber ring of the host cortex. When the phloëm of the host is reached, and especially the cambium, the cell walls of the sinker become somewhat heavier and the end cells shorter than corresponding ones of the cortical haustoria (Fig. 10). The host cells just in front of the tip of the sinker in the cambium or in the bast present a curved appearance as if under pres-

sure. It is not likely that the sinker absorbs the adjacent tissue of the host to any extent because no evidence of this was seen, and, further, there is an absence of epithelial cells, or of cells having that general character, in the sinker. The cells of the young sinker which correspond in position to epithelial cells of the cortical haustoria are cubical, and thick-walled. No cells in mature sinkers exhibit epithelial characters; the change in structure and in function of these cells takes place in the meristematic region of the host.

A cross section of an oak branch to which a mistletoe is attached shows that the sinkers of the parasite take the position of the host's medullary rays, and that the structure of portions of the sinker varies according to their relative positions. The part of the sinker which is in the cortex of the host agrees very well in structure with the cortical haustoria, but that portion which is within the xylem has a different and a characteristic structure. The sinker taken as a whole is composed of a central cylinder and a surrounding cortex. The central cylinder is, in both portions of the sinker, an almost uniform structure, but the cortex is variable. The cortex of that part of the sinker that is within the cortex of the host is composed of thin-walled cells and has few intercellular spaces. On the other hand, the outer part of the sinker cortex, which is within the wood cylinder of the host, has a denser structure, and is made up of heavy-walled cells with no intercellular spaces. The inner portion of the same part of the cortex is composed of thin-walled cells between which there are small spaces. Between the two sorts of sinker cortex just spoken of, and in a position approximately adjacent to the host cambium is the meristematic portion. Here the cells are brick-shaped, relatively small, and there are no intercellular spaces. The contents of the sinker cells appear to be almost entirely composed of starch in character resembling that of the cortical haustoria. The cells of the sinker cortex remain alive in the oldest material that I examined, and they probably die only as the parts of the host adjacent to them die. The walls of all of the sinker cells which are within the cortex of the host are lignified.

The conductive tissue of the sinker is composed of a few spiral and annular ducts which are enclosed by narrow, elongated thin-

walled cells. The latter are densely filled with finely granular matter the nature of which I did not learn. I did not succeed in demonstrating the presence of sieve tubes in the sinkers; their existence may be questioned. The long, thin-walled cells of the central cylinder are gradually shortened, and their walls thickened, as they approach the end of the sinker, and they are there indistinguishable from the other cells that make up the tip. The ducts also, at the end of the sinker, merge into the cells that compose it, so that there is a gradual transition from the cells of the central cylinder to those of the end of the sinker. The cells at the end and on the margin of the sinker are in contact with the host ducts and the union is such a close one that there is apparently only one cell wall between them. The pits of the sinker are in apposition with those of the ducts (Fig. 11) and the status of the parasite as a partial, or water, parasite, is thus established.

In the region of the cambium of the host, as has already been mentioned, the sinker cells are smaller and with thinner walls than those either toward or away from its tip. These cells have large nuclei and dense protoplasmic contents. They are typical meristematic cells. The thickness of this part of the sinker is somewhat more than that of the cambium of the host adjacent to it. By the means of active cell division in the meristematic region of the sinker it is able to accommodate its length to the increasing diameter of the oak branch. And it is also possible that the elevation of the aërial haustoria from the host is in part accomplished by the same agency.

Longitudinal and cross sections of the sinker in the region of its meristem show that the thin-walled conductive system does not unite with the phloëm of the host, sieve-tubes do not unite with sieve-tubes as in complete parasites. There is, however, a transfer of foods from the phloëm of the host to the sinker as in the cortical haustoria, but it takes place by osmosis only, because there do not appear to be any cells of the sinker with epithelial characters. The sinker, because of the lack of cells for digestive purposes, does encroach upon the phloëm of the host. This is shown by longitudinal sections (Fig. 12).

The aërial haustoria are those cortical haustoria which have become more or less freed from the host cortex, are partly or

wholly exposed to the air, and have undergone marked changes in structure and in function. As the cortical haustoria increase in bulk and occupy a larger and larger area in the host cortex, the flow of foods and food materials from the central to the more peripheral portions of the cortex is gradually checked, and the outer cells of the host cortex die. The inner cells of the host cortex, however, remain alive, and may form cork cambium between the aërial haustoria and the xylem of the host. By the multiplication of the cortex cells beneath the aërial haustoria, a considerable pressure is brought to bear upon the haustoria, which is exerted in such a way as to tend to push them away from the host branch. A flattening beneath the haustoria of the host cortical cells in question shows this point very plainly.

Parallel to the decadence of the superficial host tissues a change is noted in the structure of the cortical haustoria. This is first seen in the epidermis. The outer walls of the epidermis become greatly thickened and take on the bronze color peculiar to the exposed portions of the plant. This, especially the latter, applies to the parts of the epidermis which are exposed to the air. In sections through the edge of the dying cortex and also through the epidermis of the haustoria, the formation of the cuticle as well as the deposition of the coloring matter in it, under the influence of the light, may easily be seen. Except for the greater irregularity, the absence of trichomes and of stomates, the epidermis of the aërial haustoria agrees very well with that of the stem.

The structure of the cortex of the aërial haustoria is also in the main like that of the stem, but the cells of which it is composed are more irregular in form and in size. Grit cells and crystal-bearing cells are present in the cortex.

Cross sections of the wood cylinder of the aërial haustoria have a striking appearance, which is caused by the unsymmetrical growth of its members, the secondary growth in diameter taking place on one side, toward the outside of the stem of the host, more than on the other. The elements of the central cylinder of the haustoria resemble those of the stem, but the pith, the primary vessels and the central ring of sclerenchyma are wanting. The peculiar structure of many of the fibers, by which they resemble slime canals, and which was spoken of as occurring in the stem,

appears in the wood cylinder of the aërial haustoria. However, in the latter case the canals appear to be permanent. This point needs further investigation.

The phloëm consists of bast parenchyma, of sieve tubes, and companion cells. The sieve plates were difficult to demonstrate. The primary hard bast bundles, typical of the stem, are, of course, not found in the haustoria.

In comparing the mass of cortex with the mass of conductive tissue in the cortical haustoria with the same in the aërial haustoria we see a decided difference—the cortex preponderates in the former, the conductive tissue in the latter case. This is correlated with the change which these haustoria have undergone in function. An index of this change is found in the contents of the cortex of the two sorts of haustoria. Starch grains are found in the cortex of the cortical, but they are not present to any appreciable extent in that of the aërial haustoria. That is, the cortex of the aërial haustoria has ceased to function as a food reservoir. The great development of conductive tissue is also indicative of the change from an absorbing organ to a conductive one.

In concluding this account of the haustoria of the mistletoe it should be said that each of these kinds of haustoria are present in the older plants as well as in the young, and in this regard the American mistletoe does not agree with the European species (*Viscum album*). In *Viscum* there is a sort of tap root from which the lateral roots, cortical haustoria, spring. Frank * does not mention the formation of aërial haustoria in *Viscum* and he intimates that such, indeed, are not present, because he says that the connections between the sinkers and the stem, the aërial haustoria, are sooner or later broken. Although I have not made a close study of the oldest plants, I believe from the manner of the formation and development of the aërial haustoria that in the American mistletoe that connection during the life of the plant is never broken. This must necessarily be the case since the aërial haustoria become an integral portion of the stem.

* Frank, Die Pflzplanzen, Krankheiten der Pflanzen, 1896, p. 530.

### 4. SOME BIOLOGICAL CONSIDERATIONS

In concluding this sketch of the anatomy of the mistletoe it need hardly be pointed out that, whatever may be the nature of the stimuli, varying pressures or what not, which bring about the characteristic structure of the mistletoe, it is for the most part typical of xerophytes in general. It is to be pointed out however, that the extremely heavy walls of the parenchyma is a feature found in many leaves, and stems of herbaceous species, which live through one or more winters, or inclement seasons. Similar structures are to be seen in coniferous leaves, as well as in leaves of some orchids such as *Aplectrum*. It is also to be said that such strength of wall would give rigidity to the stem during seasons in which turgescence in these cells is an impossible condition.

In the consideration of the growth of the leaves it was shown that they did not reach the normal thickness until the second season, and the mature size was not attained until an indefinite time after that. The youngest leaves are illuminated from one side, the ventral, only, and Fig. 3 shows very imperfectly that there is a corresponding difference in the time of development of the two parts. The portion toward the light appears to have a structure somewhat more fully differentiated than the opposite side. In the mature leaf both surfaces are equally exposed to the light, and show equal development.

Among the many questions which come up for solution in a study of this kind, and which belong to the purely biological side of the general problem, may be counted those which concern the nature of the association of the mistletoe and the oak. Is the relationship between the two entirely of advantage to the parasite, or does the oak also derive benefit from it as is apparently the case in *Viscum album?* * It is clear that at the season of the year when the oak leaves have fallen, and when the plant no longer makes food, the mistletoe might be called upon to give up a portion of the food, which it was manufacturing, to the support of the host. As far as I could learn, however, such is never the case. Material collected at such a time was examined and it was found

* Gaston Bonnier, Sur l'assimilation des plantes parasites à chlorophyll, Comptes Rendus, Paris, 113: 1074–1076.

uniformly that those parts of the parasite which are the reservoirs of food contained apparently the usual amount, and that the adjacent oak tissues did not show in any way that food passed to them in the manner described. When the structure of the parasite and its relation to the oak are considered it will appear that there is really little opportunity for such a transfer of foods. The parts of the mistletoe that contain food are either in contact with the lifeless host cells (the ducts of the wood), or they are adjacent to host cells which, at the time, are dormant.

The usual conception of the mistletoe as a semi-parasite, or a water parasite, is for the most part a perfectly correct one. But the degree of parasitism varies with the age of the plant, and with the portion of the plant under consideration, for although the main part of the parasite lives on the water and the mineral salts in solution which it gets from the conductive system of the host and the carbon that it gets from the air, a small portion of the cortical haustoria depends upon the host entirely for its food and is therefore totally parasitic. The first assertion, that the degree of parasitism varies with the age of the plant, remains to be demonstrated, but there seems little question that the seedling is a total parasite, just as the cortical haustoria are. In this connection it may be of interest to point out how such a total parasite as *Arceuthobium* may have arisen. *Arceuthobium* lives in the cortex of its host, it gets food already elaborated, and its only appearance in the air is when it sends out the fruiting stalks. Now, if the American mistletoe should acquire the habit of remaining a longer and longer time after germinating in the cortex of the host, either because of difficulty in penetrating the xylem of its host, or for any other reason, it might gradually lose its power of carbon assimilation and become a total parasite like *Arceuthobium*.

The immediate effect of the parasite was not studied, but the ultimate effect, in all cases that came to my notice, is to cause the death of that part of the host which is beyond. There does not, however, appear to be any such striking malformation as in the *Arceuthobium*, or in another species of *Phoradendron* that grows on the juniper (*P. bolleanum*). *Viscum* also causes the decay of the host tissues and in this resembles *Phoradendron villosum*, but the effect is brought about in quite a different way. In *Viscum* the

sinkers that have severed their connection with the main part of the parasite through the death of the cortical haustoria, so choke the passages of the host's conductive system that growth ceases and it eventually dies from starvation.* In the American mistletoe, on the other hand, the destruction of the host tissues is brought about by the living sinkers which, while still attached to the cortical, now become the aërial haustoria, occupy the places of the medullary rays (Fig. 8) and absorb so much water that the more distal portions of the host are starved. The position which the American mistletoe often occupies at the extreme tip of a limb is brought about in the manner described with the further note that the parasite may extend its haustoria to include within its grasp the branch of which the one on which it germinated was an offshoot (Fig. 7).

COLUMBIA UNIVERSITY, March 13, 1901.

## Explanation of Plates

### PLATE 27

1. A cross section of a leaf the same age as the leaf of Fig. 4, showing a stomate, × 220.

2. Surface view of stomata to show the relative size: *O*, oak, *M*, mistletoe, × 220.

3. A cross section made in April of a leaf of the first season: *D*, dorsal surface, *V*, ventral surface, × 76.

4. A cross section of a leaf of the second season made in the spring before the growth in diameter was completed. A few cells with calcium oxalate are shown, × 76.

5. A cross section of a stem of the same age as that of the following figure, with a characteristic sunken stomate, × 220.

6. A section of a rather young stem showing the great development of cuticle, × 320.

7. Oak branch and mistletoe attached: *m*, mistletoe; *Ae*, aërial haustorium; *b*, the branch upon which the mistletoe germinated, the end of which is indicated by the dotted lines. Two thirds natural size.

8. A cross section of an oak branch with a mistletoe. The cortical haustoria have surrounded the wood cylinder of the oak, and sinkers penetrate it from every side; *S*, sinkers, × (*ca*) 2.

### PLATE 28

9. A section through the epithelial region of a cortical haustorium; *P*, parasite; *H*, host, × 220.

* Frank, *l. c.*

10. A longitudinal section through the bast of the oak and the tip of a young sinker, the cells of which have for the most part lost their epithelial characters: *P*, parasite; *H*, host, × 220.

11. A longitudinal section of the tip of a sinker, radial of the wood cylinder of the oak, which shows the apposition of the pits in the walls of the ducts and in those of the outer cells of the parasite: *S*, sinker; *O*, oak; *D*, ducts of oak; *p*, pits of host and parasite in apposition, × 320.

12. A longitudinal section, partly diagrammatic, of sinker, cross section of the oak, showing the effect of the season's changes in pressure of the oak wood cylinder; *S*, sinker; *C*, cortex of oak with the fiber rings indicated by dotted lines; *cam*, oak cambium; *Sp*, spring; *Su*, summer wood.

13. A partly diagrammatical sketch of cortical haustorium in oak cortex. The arrow points to the center of the oak stem: *P*, parasite; *C*, oak cortex; *Sc*, sclerenchymatous cells.

# A Project for Phytogeographic Nomenclature*

By Ch. Flahault

The rôle of botanic geography is relatively simple. Whatever may be the extent of the territory considered, it proposes to establish statistics of the species which inhabit it, investigate their origin, their migrations and their present and former distributions. It is desirable that in immense countries like the United States of North America, or Russia, on a desert island or in a province, writers may be enabled to employ the same terms to designate the various subdivisions of importance without being misunderstood. Russian botanists divide all the European territory of the Czar's empire into four regions; a recent author recognized six in the little island of Lesbos, the extent of which does not exceed several square kilometers.

While it is unfortunate in some respects that the meaning of a word lacks precision, the subject itself explains enough of that which is in question to cause no serious trouble in the variation of the interpretations; it is easy to return to the subject in question.

This incoherency is the more to be regretted when it occurs in works on botanic geography. Phytogeography becomes more and more an exact science; its principal aim is to make known the multiple relations of vegetation to an environment however varied. To express these relations it is important, then, that we have an all-sufficient vocabulary on which those interested would agree. This is an essential condition to all progress. Now, the greatest disorder prevails in works on the subject of nomenclature and on the subordination of geographic groups. Some use the same term promiscuously for great extents of country and for elevated mountain zones. For some, zones are tracts of land characterized by forms of vegetation peculiar to plains, while regions are applied to the mountains; they say forest region, subalpine, alpine, nival regions, etc. For others, regions are territories in the plains distinguished by peculiar vegetative and floral characters;

*Translation of a paper read by Professor Flahault at the International Botanical Congress, Paris, October, 1900.

region of the steppes, region of coniferous forests, etc. This idea of botanic region, so diversely interpreted, designates geographic units of a superior class, or it is not subordinated to others according to the meaning given it, so that the names of regions, provinces, zones, districts, sectors, etc., designate very different things according to the authors who use them.

A. Engler * has adopted a series of names for phytogeographic units of different classes; but he has not been followed by the majority of botanists, notwithstanding the authority of his writings, as possibly this series does not meet with the requirements of a science which demands more and more precision. Without any doubt, in 1879, Engler did not pretend to regulate a question of method, not wishing to establish a code of phytogeographic nomenclature, *ne varietur*. He intended, it seems to me, only to express clearly the facts which are the object of his memoir; he has chosen the terms that he employs, simply because they appear the most convenient to him, without discussing all their advantages or inconveniences.

The time has come when it appears necessary that a technical terminology should be established or we shall no longer understand each other. A comparison of facts will be facilitated if we adopt a common basis and a sufficient uniformity of expression. We will be enabled to compare comparable units if we restrict the same name for units of the same value. We will be able under these conditions to speak of the temperate regions with or without a dry season; we will be able to draw a parallel between the Mediterranean, Australian, Cape, Californian and Chilian *regions*, the desert *domains* of northern Africa, of western and central Asia, of Australia, of Colorado and Mexico, the *district* of the Vosges and of the Maures, the subalpine and alpine *zones* of the Alps, the Pyrenees and the Caucasus, etc. Dr. O. Warburg, at the geographic congress of Berlin insisted on the necessity of such an understanding as soon as possible.

This article does not pretend to solve the problem; but if the time has come for a statement, the Botanical Congress furnishes an opportunity which must not be allowed to pass. It does not appear useless, at all events, to propose some principles and to advance

* A. Engler, Versuch einer Entwicklungsgesch. der extratrop. Florengebiete.

some ideas, in order to elicit thoughtful discussion, here and elsewhere.

Phytogeographic nomenclature may be applied to two different things:

1. To geographic and topographic substrata of vegetation, *i. e.*, to *geographic and topographic units.*

2. To vegetation itself, grouped in different ways, according to conditions of climate and environment, *i. e.*, to *biologic units.*

Let us then direct our attention to the first.

## I. NOMENCLATURE OF GEOGRAPHIC AND TOPOGRAPHIC UNITS

It will be expedient to take as the basis of fundamental divisions, essential facts which dominate all others and which are incontestable in themselves and in their reactions on vegetable life.

The general relations of vegetation to the fundamental conditions of climate need no discussion here. Prof. Drude* was right when he endeavored to represent the fundamental climatic data in such a way as to correlate essential biologic facts with their determining causes. Our lithosphere may thus be subdivided by lines more or less parallel to the equator, into zones distinctly characterized at the same time by climate and by the vegetation which is its expression. In cold countries there is a corresponding form of vegetation, plants of small size with highly developed underground organs, etc.; plants which inhabit them resist very low temperatures during their period of rest, and even during their vegetative period endure temperatures below 0° C.; these are microthermal plants. In warm countries there are corresponding plants which require very high temperatures, perishing at 0° C. or even at temperatures above freezing point; many of them have their activity scarcely interrupted. These are macrothermal vegetations. In temperate countries there are plants which undergo a periodical rest, and which alternately endure low and high temperatures; these are mesothermal.

It is natural then to divide the terrestrial globe into cold, temperate and warm zones, as did William Schimper† following Grisebach. Without becoming unintelligible, distinction may be made

* Drude, Manuel, p. 69, pl. iv.

† Schimper, Pflanzengeographie, 227.

between the cold and temperate zones according to the hemisphere which they occupy. Prof. Drude has done this for the general grouping of the regions of vegetation in publishing sheet 46 of Berghaus' Physical Atlas.

This grouping is only of general value. It permits a first separation, a division of the earth comprehensible to persons who are not prepared for special study. It is destined only to facilitate subsequent grouping, to render it even possible. The tropics are not the limits of the tropical flora; the Arctic circle does not indicate exactly where certain floras either commence or end; for which reasons it seems preferable to express the most important climatic character of each of these zones, to distinguish them simply under the names of warm, temperate and cold (in place of tropical, temperate and arctic). In this case, the word zone is used in the sense that is generally given it in French.

The definition of zone exactly applies to these units of the first order; they are divisions of the sphere's surface included between two parallel lines; this is the signification of the word as adopted by meteorologists, but it seems impossible to us not to apply it to the belts following which the mountain flora becomes divided. Another term cannot be found to replace it; that is why this point will have to be reconsidered later.

The great warm, temperate and cold zones are respectively divided into less important groups. Climatic causes combine in each fundamental zone in different methods, to effectuate, on the whole, very different climates, to allow the development of vegetation of varied aspect and composition. The differences in the character of vegetation of two neighboring countries explains the dissimilarity of their climates, and their resemblance is the expression of their joint climatic factors. In other words, a like ensemble of climatic conditions combining in the same way determines a like *type of vegetation;* other conditions, or only another division of the same conditions, give occasion for the development of types of different vegetation. So it is that the vegetative type of our western Europe is that of the forest composed of trees with deciduous leaves; while that of eastern Europe is the steppe; that of the warm and constantly humid climate of the tropics, is the forest which is always green.

Thenceforth, the fundamental climatic zones divide naturally into large natural *regions of vegetation.* When studying the flora of the world, this division is the most apparent, and it is the most important. The great regions of vegetation are great climatic regions; the map of the distribution of large natural groups coincides with the principal types of climate over the whole earth.

Martius was the first to distinguish regions (Florenreiche).* A. de Candolle defined them with more precision.† The name has been generally adopted; there is then reason to follow tradition. A more or less broad sense has been attributed to it. We think it would be expedient to give it the import which was attributed to it by Grisebach in his principal work.‡ The vegetative regions of Prof. Drude are the same.§ So we say the *Forest region of northern Eurasia*, the *Temperate forest region of western Europe*, *Mediterranean region*, *Eurasiatic steppe region.* This is the proper meaning of the word in French; it expresses above everything a "large extent of country" (Littré). The great mountain masses considered as a whole and in their relations to the regions which surround them and to the entire terrestrial surface may also constitute natural regions. The entire group of the Alps constitutes the *Region of the Alps;* the *Region of the Caucasus* is distinguished in the same way, also that of the *Pyrénées*, the *Iberian group* and of the *Balkans.* It will be a question if, according to their relative importance and the relation of their vegetation to that of adjoining units, mountain groups of less importance should have the value of different subordinate units. So that we would say: the domain of the central group of France, domain of the Jura, austro-occidental domains, the central and eastern of the Alps; that we distinguish eastern, central and western sectors of the Pyrenees, the Savoie, Dauphiné, Provençal and Maritimes sectors of the Alps, the districts of the Albères, the Causses and the granitic Cévennes, etc.

The different strata of vegetation which range in echelon over the declivities add a certain number of questions to those which

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* Von Martius, Historia Natur. Palmarum, 1: tab. geogr. III. and IV., 1831.

† A. de Candolle, Introduction Géogr. bot., 1837.

‡ Grisebach, La Végétation du Globe.

§ Drude, Manuel, p. 302.

make up the whole, projected, as it were, on the general surface of the globe, in diversifying biologic conditions and in multiplying phytogeographic problems.

The great fundamental zones are subdivided then into vegetative regions which constitute the most important phytogeographic units. The idea of zones in general answers the need of synthesis and results from a consecutive comparison. The polar tundras appear to us a region contiguous to the forest region of northern Europe before we consider whether each of them should not be classed in a different superior group.

It being so, and because it appears necessary to reserve the name of zone to express parallel belts following which the mountain vegetation is divided, it seems advantageous to give the name of *Groups of Regions* to the fundamental zones.

So we would have a group of cold regions, one of temperate and another of warm regions; the same could be said of groups of boreal, austral and tropical regions.

It has been said that this primary grouping has for its principal purpose the facilitating of a grouping of the second order; it is, therefore, arbitrary; it suffices to make it good that it depends on evident and incontestable facts.

Botanic regions may be subdivided into secondary circumscriptions of variable extent in the determination of which the variations of climate are also secondary, but which depend ordinarily on topographic and geographic conditions.

Thus in the forest region of western Europe, the Atlantic Coast countries are clearly distinguished from the lowlands bordering on the North Sea and from the valleys of the Rhine and Danube. The Mediterranean region south of the Pyrenees has not the same character as in France or in northern Africa.

To these subdivisions of regions Prof. Engler has given the name province; in many countries this word has an administrative or political sense so that its use would give rise to ambiguities. The word *Domain* seems more appropriate.

In the forest region of western Europe there is distinguished then an *Atlantic domain*, a *domain of the plains of northern continental Europe* and one of *central Europe;* in the Mediterranean region there are the Iberian, the Mauritanian, French domains, etc.

Domains themselves may be divided into *sectors;* secondary climatic characters interpreted by vegetation will be taken into account, but the consideration of botanic elements of which we have not had to take account until now, also intervenes. When a portion of a region or a domain may be characterized by a certain number of plants which have entered from other countries, it would constitute a *sector.* In the Atlantic domain an Aquitanian *sector* may be distinguished where there are numerous species which have immigrated from the Mediterranean region, and where these fail, an Armorican *sector;* in the French domain of the Mediterranean region, there is a Provençal *sector* where representatives from the Italian domain are abundant, Roussillon and Corbières *sectors* which have been invaded by Iberian species, notwithstanding the barrier of the Pyrenees; in the Iberian domain an Andalousian *sector* characterized by many Moorish species, etc.

A new distinction may be introduced based either on geographic or topographic causes or on the physicochemic characteristics of the soil influencing vegetation.

*District,* such as we understand, it together with Prof. Briquet, corresponds to the *Bezirk* of Prof. Engler.

Islands separated from adjoining land by more or less extensive arms of the sea become characterized as districts by the appearance of endemic types. Ridges, exceeding the limits of vegetation, which separate valleys, tend to give to them special characters by preventing migration and in favoring endemism. Mountain ranges of a known mineralogic composition, isolated in the center of a group of different composition, may often be distinguished as districts for the same reason. C. Schröter, John Briquet and Paul Jaccard cite excellent examples of such in the Alps.

In the French domain of the Mediterranean region there are included the calcareous *district of the lower Corbières,* the siliceous volcanic rocky *district of the Maures and the Estérel,* while that of the *Balearic Islands* with their many endemic species, makes a very distinct district in the western sector of the Iberian domain.

*Subdistricts* may also be distinguished if they prove useful after a careful analysis. It is possible that some day the opportunity

may be recognized of distinguishing two subdistricts in the district of the Maures and that of the Estérel, if with the mineralogic differences between the ancient and modern eruptive soils are corresponding botanic differences, which have escaped us as yet.

Prof. Briquet has distinguished several subdistricts in the western Alps and in the Jura.* In France for the same causes, and probably in all countries of ancient civilization where the soil has retained the impress of history, botanic districts often coincide accurately with the ancient "country." In mountain groups the subdivisions recognized by the inhabitants also represent the natural divisions of districts. The names of countries and of mountain groups which are used by the population may often be given to indicate districts or subdistricts without resulting error or ambiguity.

The last term remains to be spoken of, that of *station*, the final one of the series of geographic and topographic units.

In 1844, Wimmer† insisted on the necessity of adding to the morphological diagnosis of each species a phytogeographic description "which will determine with precision and in definite terms all environmental conditions; for a description of this kind contributes not less than the first to a knowledge of the species."

A station is a circumscription of any extent, but oftener limited, and represents a complete and definite ensemble of conditions of existence. Station sums up all that is necessary to the species which occupy it, the combination of climatic and geographic factors with the edaphic and biologic factors, that is to say the relation of each species to the soil and to associated species.

The disappearance or only the modification of an element, a specialization or even a very slight variation of any factor would be sufficient to determine a difference of station. The vocabulary of each country, born of the environment and need that puts a people to the test of expressing facts and phenomena which they observe each day, should furnish the means of designating stations peculiar to the country. The Scotch heaths, the Russian steppes, the moors of Brittany, the prairies of North America, the "près-bois" of our Alps, represent peculiar forms of vegetation which

* John Briquet, Rech. sur la flore du district Savoisien, 1890.

† Wimmer, Flora der Schlesien, 1844.

may give rise to errors, for those unaquainted with them might deem it possible to correlate them with a form of vegetation of another country. It is necessary then in botanic geography to mistrust translations and not fear to adopt the name of a station which has been furnished us by the indigenous language.

The conception of Savannah as adopted and popularized by our travelers comprises, it appears, varied stations, that the ignorance of botanic geography alone makes confusing. It is important then to accept indigenous names as having a geographic value where their exact synonym is not known in one's own language.

The polar *Tundra*, the Siberian *Taïga*, the *Myrar* of the Swiss, the *Watten* of the coast of the North Sea, the *Llanos*, *carrascos*, *campos*, *potreiros* and *pinhals* of Brazil, the *scrub* of Australia have no equivalent in our language and these names have the same claim for preservation as our *garigues* and *maquis*.

It even happens (and this is the case in our own French language) that far from it being necessary to translate words given to natural features in other languages, the admitted classic vocabulary is not sufficient to explain facts and phenomena which are exhibited in a country, or the objects which are there encountered. In contrast with other languages which are profoundly penetrated by the poetry of nature, resulting from the constant contact of man with nature, our own, however literary and erudite, originating in the salons where polished society formerly gathered, has no words to express that which it has not known. It is from our old language that the words garigue and maquis have come. *Sansouire*, *Erme*, *Casse*, *Campas* have been acquired from ancient dialects. They express things of which our literature has no idea. It is proper to so enrich our language.

In finishing the nomenclature of geographic and topographic units only a few words remain to be said to express the more or less parallel bands which different vegetations follow when they are superimposed in the altitudinal sense.

If a certain parallelism in climate exists between the regions which extend from the equator to the poles and that of mountains considered from their base to their summit, it is now known that this parallelism depends only upon the temperature of the air. Therefore there is no need for them to be confused. Now in France,

the word *zone* expresses a space which is clearly limited, as for instance that portion of a sphere's surface which is contained between two parallel lines (and accordingly this name agrees with the fundamental climatic-botanic zones) as a space is compared to a band. The word is used in this sense in geology, astronomy, meteorology and in military science. With this precise signification it expresses better than all others successive stages of vegetation from the base to the summit of mountains. In this exact sense the word has been adopted by French phytogeographers. "At an elevation of 11,000 feet, said Edmond Boissier, in 1839, one may expect to find vegetation distributed in distinct *zones* and this is what actually happens, but settling the delimitation of these *zones* offers many difficulties.* * * *" * Dr. Christ has likewise adopted this French interpretation of the word zone when he says that "the differences which occur in the plant world when we ascend from the plain to the snow limit convey to us the principle of *zones*. It is sufficient to cast a glance even from a distance over one of the chains of our Alps to ascertain that the vegetation which covers it is separated into very distinct *zones* with well-accentuated delimitations.†

Let us sum up all that has preceded by enumerating only the series of units covering the general surface of the globe, such as we think possible to subordinate one to another:

1. **GROUP OF REGIONS.**
2. **Regions** (Martius, 1831).
3. **DOMAIN.**
4. **Sector.**
3. DISTRICT (Bezirk, Engler, 1879).
6. SUBDISTRICT.
7. *Station* (Wimmer, 1844).

The word zone would be applied only to those stages of vegetation which are superimposed in altitude, according to the signification given to it by Boissier in 1839.

## II. NOMENCLATURE OF BIOLOGICAL UNITS

The nomenclature of biologic units is more simple *a priori*. It is necessary to recognize, however, that although the disorder

* E. Boissier, Voyage dan le midi de l'Espagne, 1: 185. 1839.

† H. Christ, La Flore de la Suisse et ses origines, 12. 1883.

is great in the classing of geographic and topographic units, in biologic units it is extreme. To avoid being misled in this labyrinth it would be well to retrace our steps in the course that we have just followed and consider first the elementary units, those which populate stations. It is very encouraging that good works which have been published during the last few years have commenced to introduce order into the subject by making *Associations* the foundation of critical study of botanic geography.

I did not pretend to make an innovation when I insisted, in 1894, on the necessity of taking the associations of plants living in common in the same station as a starting point for phytogeographic comparisons. It is due to Humboldt that attention was first called to the importance of *Plant Associations*. In his *Essay on the Geography of Plants* * in 1807 he showed that the different associations of plants which succeed one another from the base to the summit of Chimborazo depend strictly on temperature, humidity, atmospheric pressure, etc.

In 1820, A. P. de Candolle † urged the necessity of noting all details relating to associations: the station and its local variations, the degree of frequency or rarity of plants, etc., and their grouping into societies.

This conception therefore has its history. It is necessary that the significance of the term should be precisely stated. Vegetable association is the final expression of vital competition and of adaptation to environment in the grouping of species. Plants which inhabit the same station are not only connected one with another by simple relations of coexistence, but also by a bond of reciprocal interest, for certain of them receive benefit and profit from the conditions caused by the presence of others. The term vegetable association does not imply the harmonious coöperation of diverse tendencies toward a common end of collective advantage, as in all society founded on the principle of division of labor. It applies to the bringing together of specific and morphologic forms which are foreign to one another, for the exclusive profit of each individual; they live side by side, following the conformity or diversity of circumstances that suit them, either in the actual conditions of

* Al. de Humboldt, *loc. cit.*, 1807, p. 14.

† A. P. de Candolle, Projet d'une flore physico-géogr. de la vallée du Léman.

the environment or in the conditions determined by the presence of other plants.

Among the species which go to make up the association, some are *dominant*, either by the action they exert on the habitat in creating, as it were the station, or because they are characteristic of the plants of the country, in the form, size, or numbers of individuals; they form then the foundation of the vegetation. Others are *secondary*, more or less isolated, as if they had been scattered over the fundamental vegetation; or else are they *subordinated* in various degrees, either because they are scarce or rare, or it may be that they cannot live except in the shelter of the first, in their shade, as epiphytes on their aërial organs, or at their expense as parasites. They can also be subordinated by the limited duration of their active life (annuals, biennials, bulbous plants, etc.). The dominating species always characterize the association.

Association, so understood, answers exactly to what we have admitted since 1893, to that which has been described as such by E. Warming, in Denmark; Kerner, in Austria; Robert Smith, in Scotland; F. Höck, in Germany; Schröter, in Switzerland.

The term *Association* (*Plant association*) has been applied to it by English-speaking botanists. Warming called it *Plantesamfund* (in Danish) *Pflanzenverein;* Kerner described it under the term of *Genossenschaft;* Höck also called it by the name of *Bestand.* There are nevertheless divergences of opinion in regard to *Association.* W. O. Schimper regards it as composed of special ecologic groups: "It is the union of plants dependent on one another, some of which have always a dependent character and are unable to live without the help of others."* He recognizes four kinds of ecologic associations of this sort—lianas, epiphytes, saprophytes and parasites; these are groups of biologic forms, not of associations as understood by A. P. de Candolle and Humboldt.

If association is the simplest biologic unit from the geographic point of view, the ultimate expression of the struggle for life and adaptation, biologic forms may be considered as elementary units from a special ecologic point of view, as species are the elementary units which the botanist employs.

Mr. Warming has brought into correlation with the state of our

* W. O. Schimper, Pflanzengeographie, 208. 1898.

biologic and physiologic knowledge, the term *biologic forms* (*Lebensform*, *Vegetationsform*) which was previously but vaguely understood.

Grisebach understood by it forms of the same character which may or may not have morphologic affinities. It is known now that environment influences structure; this conception has been given precision. For example, when we speak of the ericaceous form we do not intend to treat only of the physiognomy, but also of a number of details of structure of which the outward appearance is but the collective expression.

Grisebach, in giving a vague meaning to *biologic form*, did not think of defining more clearly biologic groups which had as a basis the vague definition of biologic form such as he had conceived it. In 1838 he endeavored to group them under the name of *Phytogeographic formation* (*Pflanzengeographische Formation*, *Vegetationsformation*). "*Natural formation* includes plants which may be very different, but which have properties and characters in common, which may be summed up by pointing out several species which exemplify the special characteristics of the whole." So understood, forest, prairie and steppe are natural formations. But taking up this definition again to introduce more and more specious distinctions, Grisebach in 1872 distinguished fifty-four formations. Prof. Drude enumerated twenty-seven in the hercynien group.* In 1896 he distributed the different forest types of Germany into fourteen formations.† Kurz saw eight formations in the forest of Burma.‡ Hult divides the vegetation of northern Finland into half a hundred formations.§ The primitive idea has disappeared; thanks to the new interpretation, the ensemble disappears under the details, the tree hides the forest.

This diversity of interpretation has caused great difficulty in expressing facts relative to botanic geography.

Our forests, whether they be composed principally of oaks or of beech, or oaks and beech trees mixed, or associated with hornbeams or maples, etc., correspond none the less to a uniform type.

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* Drude, Ueber die Principien . . . 1889.

† Drude, Deutschlands Pflanzengeographie, 1896.

‡ Kurz, Forestflora of British Burma, 1877.

§ Hult, Försök till analyt. Behandling, 1881.

This is properly a same *Formation* in the primitive sense of the word. *Association* alone is modified by dominant species and with more or less extended variations that their absence or presence introduces into the relationship of members of the association. Our "moors" of the north and west constitute a formation of the same kind, where the dominating species may be either *Calluna vulgaris* or *Erica cinerea*. Our "maquis" are of infinite variety, a score of the 70 ligneous species of which they are composed may be either dominant or subordinate according to local circumstances.

It is necessary then to distinguish between *Formation* in the broad primitive sense given to it by Grisebach, and formations such as he understood them later. The latter are associations characterized by a physiognomic type instead of by dominant species. But as the most prominent physiognomic type is more often represented by dominant species, it often happens that formation, so understood, corresponds perfectly to association as we have defined it.

Drude, Beck, Kerner, Warming admit the broad sense but with various delimitations; R. Hult, Stebler and C. Schröter agree to the narrower sense of the term. Others complying with the same variations of the definition as Grisebach, have allowed intermediate interpretations.

The result is that for some the definition of *Formation* answers to a general type, as the Forest, while for others it has a special import; the forest then comprises a great many different *Formations*.

This is not all. If in Grisebach's first definition, formation had a purely physiognomic import, if the same word denotes an ensemble of extended or restricted vegetation, the confusion is increased on account of many authors wishing to give it a special signification.

Some, in fact, have reserved for formation a descriptive physiognomic sense, while others, attempting to determine the relations of cause to effect, gave to it a topographic or ecologic sense. For example, W. Schimper considers a formation to be an assemblage of plants determined by qualities of the soil; there are therefore climatic and edaphic formations. Some even interpose origin in the definition of formation, as for example, Celakovsky regards a for-

mation as a group of species which have entered a country at the same time.

It is not to be marveled at that several botanists, who had doubtless lost their way in this confusion, acknowledge having employed the word without thinking of its definition, because others had previously made use of it.

It has not been possible to enumerate all the opinions as to the meaning of the word *formation*. Between the two extremes, the first interpretation by Grisebach and that of R. Hult there is a scale of infinite shades of meaning. The confusion is like that of a labyrinth.

Kerner, however, accepted the word as a necessity "because it had been introduced into science," notwithstanding the fact that he considered it badly chosen. Warming refrained from using it and Robert Smith has followed his example; his works have gained thereby a decided clearness.* We ask that phytogeographers make a decision, but in the meantime when they speak of formation we also ask that they say exactly what they mean by it.

Meanwhile, we readily describe the word *Vegetation* as an indeterminate grouping, as proposed by Warming.

With Warming, the designation of *Group of associations* (*Vercinsklasse*) will be reserved for the designation of several associations subjected as a whole to the same general conditions of environment. The association of beech, of peduncled oak, and of the intermingled forests of our plains, etc., form a *Group of associations of tropophilous trees*. The association of *Pinus sylvestris*, of *P. maritima* and *P. Cembra*, of spruces, etc., form a *Group of associations* of resinous trees with persistent foliage.

The following groups of associations are distinguished in France:

Non-resinous trees with persistent leaves (cork and evergreen oaks).

Coniferous trees with deciduous leaves (larch).

Resinous trees intermingled with other foliage (beech and spruce, beech and Norway spruce, Norway spruce and birch).

Resinous trees and non-resinous trees with persistent leaves (evergreen oaks and Aleppo-pine, cork oak and *Pinus maritima*).

* Rob. Smith, Plant Association of the Tay Bassin, 1898. On the study of Plant Association, 1899. Botanical Survey of Scotland, 1900.

Shrubs and shrubbery with persistent leaves (garigues and maquis).

Ericaceous shrubs (heather, etc.), etc.

There are continuous groups of homogeneous associations (*geschlossene Formation*) and interrupted groups of associations (*offene Formation*) whose elements are distant from one another, dissociated, as the trees in the "prés-bois" of larches, the thickets in the Mediterranean garigues, the brush wood in the Brazilian campos, the tufts of grass on gravelly shores or on the dunes of the sea coast. The vegetation may be so thinly scattered that the name of the group of associations may be given it by the substratum.

In this way groups of plant associations could be distinguished as of the dunes and beaches of the sea coast, of rocks, of moraines, of the banks of streams and rivers, etc. These details may be easily stated in an exact manner.

Groups of associations may themselves be distributed into large ecologic series based on the uniformity of the factors which determine them, as proposed by M. Warming. There would be series of hydrophilous, xerophilous, halophilous, mesophilous groups of associations which would be designated simply by their substantives: Hydrophytes, xerophytes, halophytes, mesophytes. On this point phytogeographers have but to follow the excellent principles laid down by Warming.*

The great phytogeographic regions are characterized by a peculiar vegetable landscape, by a *type of vegetation* which reflects a distinct result of the reaction of the climate on the plants. Specific units assume the same appearance or a small number of distinct appearances; they resemble one another in aspect, height and form. The tree vegetations of temperate Europe, of North America, of China and Japan have all the same appearance. They belong to the same *type of vegetation.* The herbaceous plants of the Steppe, however different they may be from the specific point of view, have everywhere the same aspect; the tropical forest with its multiple heights of vegetation, its lianas, its epiphytes, its herbaceous carpet of infinite variety, still represents wherever it is seen, the same type of vegetation.

* Warming, Lehrbuch der oekol. Pflanzengeogr., p. 114.

Good common sense has distinguished by special terms the sum of biologic characters appropriate to each of these types. Science has but to accept them. Trees with deciduous leaves, trees with persistent leaves, shrubs, lianas, mangroves, epiphytes, fleshy plants, herbs, mosses, lichens, algae (independent of all systematic consideration) are types of vegetation. These ecologic groups represent biologic units of the first order. As we have done for geographic and topographic units, let us enumerate the series of phytogeographic terms of biologic order such as it appears possible for us to establish.

1. **TYPE OF VEGETATION** ecologic, denominated as in ordinary usage.

2. Ecologic **series** of **Groups of associations** expressed by a substantive: hydrophytes, xerophytes, etc. (Warming, 1894).

3. GROUPS OF ASSOCIATIONS (Vereinsklasse, Warming, 1894 = Formations, Schimper, 1898, Grisebach, in part).

4. ASSOCIATIONS (Al. de Humboldt, 1807. A. P. de Candolle, 1820 = Formations, Grisebach, 1872).

5. *Biologic form;* this is the simplest ecologic unit, as station is the elementary topographic unit.

I will have attained my aim if the suggestions which I have endeavored to group provoke discussion and influence all those who are inconvenienced by the disorder of phytogeographic nomenclature to agree to put an end to it.

The botanical congress will, perhaps, deem it expedient to commit the care of studying this question to a commission composed of the principal phytogeographers of different countries and invite them to pursue an inquiry, the conclusions of which could be submitted to a subsequent congress. Phytogeographers are unanimous in recognizing the importance of an agreement as soon as possible; we entreat them to be willing to unite their good offices with that object in view.

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## Proceedings of the Club

WEDNESDAY, MARCH 27, 1901

This meeting was held at the College of Pharmacy, 17 persons present, Dr. Britton presiding in the absence of other officers.

The following were elected to active membership: Mr. A. G. Agnew, 45 Wall Street; Mr. J. M. Hoffman, Tallahassee, Florida; Mrs W. E. Damon, The Chelsea, 222 W. 23d Street, N. Y.; Mr. E. L. Morris, Western High School, Washington, D. C.; Mr. James Walker, 47 Maiden Lane; Miss Mary I. MacDonald, 17 Sylvan Terrace, W. 161st St.; Miss Caroline A. Baer, 102 E. 96th Street; Mr. Roland M. Harper, 1310 Boston Road; Mr. Percy Wilson, Botanical Gardens, Bronx Park, N. Y.

The Field Committee's report for 1900, delayed by illness of the Chairman, Dr. Schoeney, was presented this evening by Mr. Eugene Smith for the committee, and was accepted by the Club. A plea was made by Mr. Smith for more volunteers to act as guides, it having often proved difficult to secure them.

The Secretary announced that the annual grant from the Newberry Fund in aid of scientific research is open to competitors this year until June 1, 1901, in geology or paleontology. Dr. Britton remarked that a friend of scientific investigation had so added to the fund as to bring its award up from $50, as before, to $100, the amount offered this year.

On motion, Dr. A. Hollick was made nominee of the Club for this award for the present year.

The first paper of the evening was by Dr. John K. Small, on "The North American Genera of Mimosaceae." Dr. Small exhibited a uniform series of diagrammatic drawings, illustrating the flowers and fruit of each of these genera, and explained his proposed classification, replacing the previous artificial grouping. The variability of the fruit in valves, margins and cross-partitions was commented on. Discussion of the common sensitive plant followed, in which it was remarked that the sensitiveness to shock is so delicate as to be stimulated by holding a burning-glass near,

or by drops of rain-water on first falling, or by holding a sponge of ammonia or of chloroform near. The utility seems unknown, except as the hot sun setting the leaves on edge prevents injury from intense sunlight. Sachs' suggestion was that the depression of the leaves served as a protection from hail; but it now appears that the native center of the plant is chiefly in the Orinoco region where hailstorms are unknown. Much energy is exhausted by folding, and it is well known that the greenhouse sensitive-plants are frequently worked to death by repeated irritation.

The second paper was by Dr. Rydberg, on "The Oaks of the Rocky Mountains." Dr. Rydberg exhibited examples of 28 species of this region. His paper will soon appear in print.

EDWARD S. BURGESS,
*Secretary.*

TUESDAY, APRIL 9, 1901

The meeting was held at the Museum of the New York Botanical Garden at 3:45 P. M., with Dr. N. L. Britton in the chair. Fifteen persons were present.

The announced scientific program consisted of a "Report of a recent visit to the Royal Gardens at Kew, England," by Mr. George V. Nash. Mr. Nash was absent about six weeks, nearly the entire time on the other side being spent at the Royal Gardens, Kew, securing specimens of living plants for the New York Botanical Garden. The collections were carefully inspected under the guidance of the officers of the institution, and such duplicate material picked out as was desired. In this way much valuable material was secured, both for the outside and conservatory collections. Many of these were procurable only at a botanical garden, and a number of them were not obtainable elsewhere than at Kew. Of the large number of plants selected, over 1000 species have already been received and incorporated in our collections, These include about 550 species of herbaceous plants, 350 shrubs and trees, and 150 succulents. The remainder of the material will follow as fast as the authorities at Kew can select it.

Dr. Britton remarked that the favor accorded by Sir William Thiselton-Dyer in permitting Mr. Nash to select duplicates of living

plants from the rich collections at Kew would be most gratefully appreciated not alone by the managers and members of the New York Botanical Garden, but by all American botanists.

Dr. Britton presented a communication on a tree new to the American continent, a white birch from the Alaskan region, collected by Mr. R. S. Williams and Mr. Tarleton, and represented in the U. S. National Herbarium also by two specimens collected by Miss E. Taylor. The tree was described by Regel as *Betula alba*, subsp. *verrucosa*, var. *resinifera*, but is evidently entitled to specific rank.

Adjournment followed.

MARSHALL A. HOWE,
*Secretary pro tem.*

WEDNESDAY, APRIL 24, 1901

The meeting was held at the College of Pharmacy with Professor Underwood in the chair. Ten persons were present and the following new members were elected: Miss May Palmer, Training Dep't, Normal College, N. Y. City; Miss Nellie Y. Pietsch, 221 East 62d Street, N. Y. City; Mr. George W. Short, 159 West 125th Street, N. Y. City; Miss Ada Watterson, Barnard College, 119th St. and Broadway, N. Y. City.

The announced scientific program consisted of a paper by Professor Francis E. Lloyd, entitled, "The Genus *Lycopodium*: A Criticism," which in the absence of the author was read by the secretary pro tem. This was a review and criticism of the treatment of the genus *Lycopodium* by Pritzel in the recently published part of Engler and Prantl's "Die natürlichen Pflanzenfamilien" dealing with the Lycopodiaceae. The paper will be published in full in an early number of *Torreya*.

Professor Underwood remarked on segregations in the *Selaginella rupestris* group, stating that Dr. Hieronymus of Berlin had recently recognized twenty-seven species in this group, ten of them American, outside of those recently proposed in this country.

MARSHALL A. HOWE,
*Secretary pro tem.*

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New species in *Arctagrostis* (2), *Calamagrostis* (2), *Trisetum*, *Poa* and *Panicularia* by Nash; in *Carex* (3), *Betula*, *Silene*, *Arenaria*, *Ranunculus*, *Roripa*, *Mer-*

*tensia*, *Valeriana*, and *Petasites* by Britton; in *Polygonum* (2), and *Saxifraga* (2), by Small; in *Plantago* by E. L. Morris, and in *Limnorchis* (2), *Salix* (3), *Erysimum*, *Astragalus* (2), *Aragallus*, *Stenotus*, and *Erigeron* by Rydberg.

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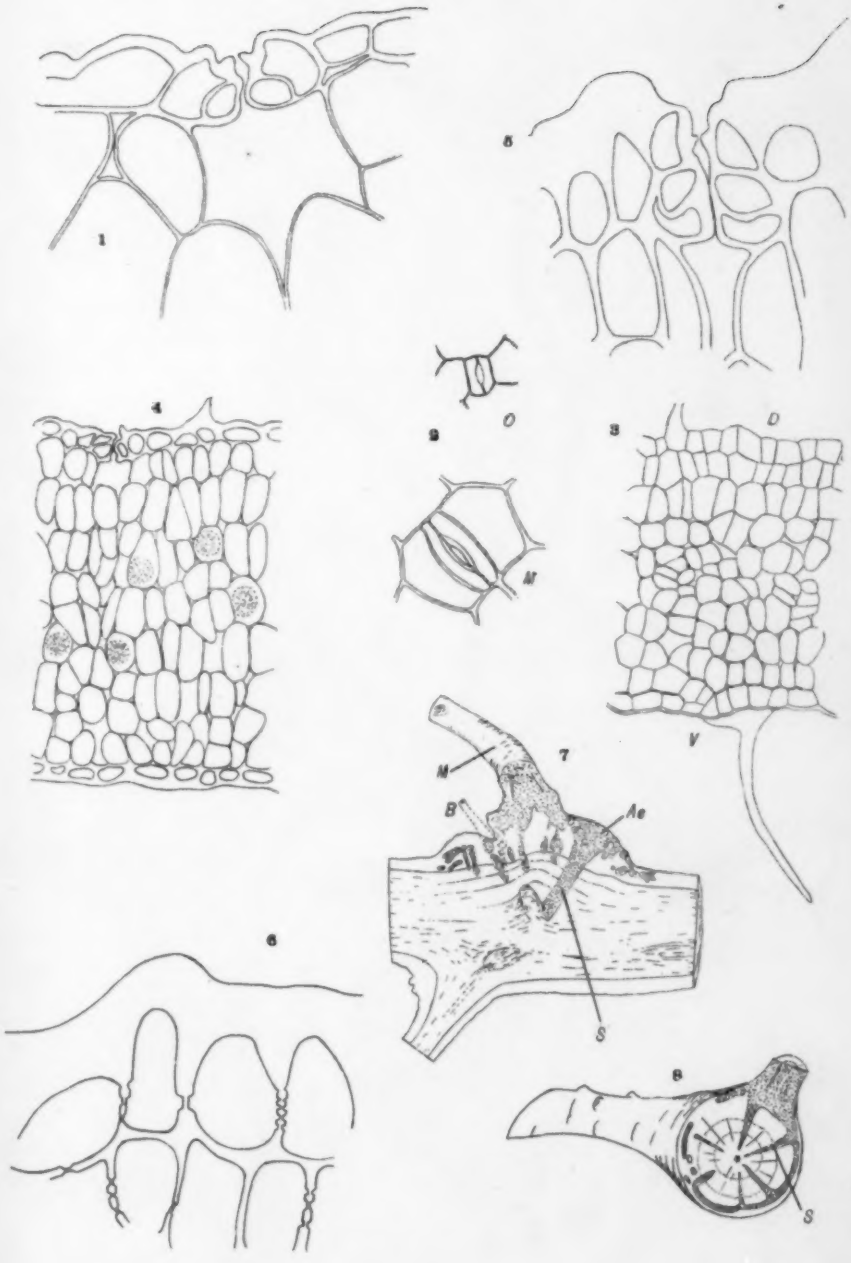


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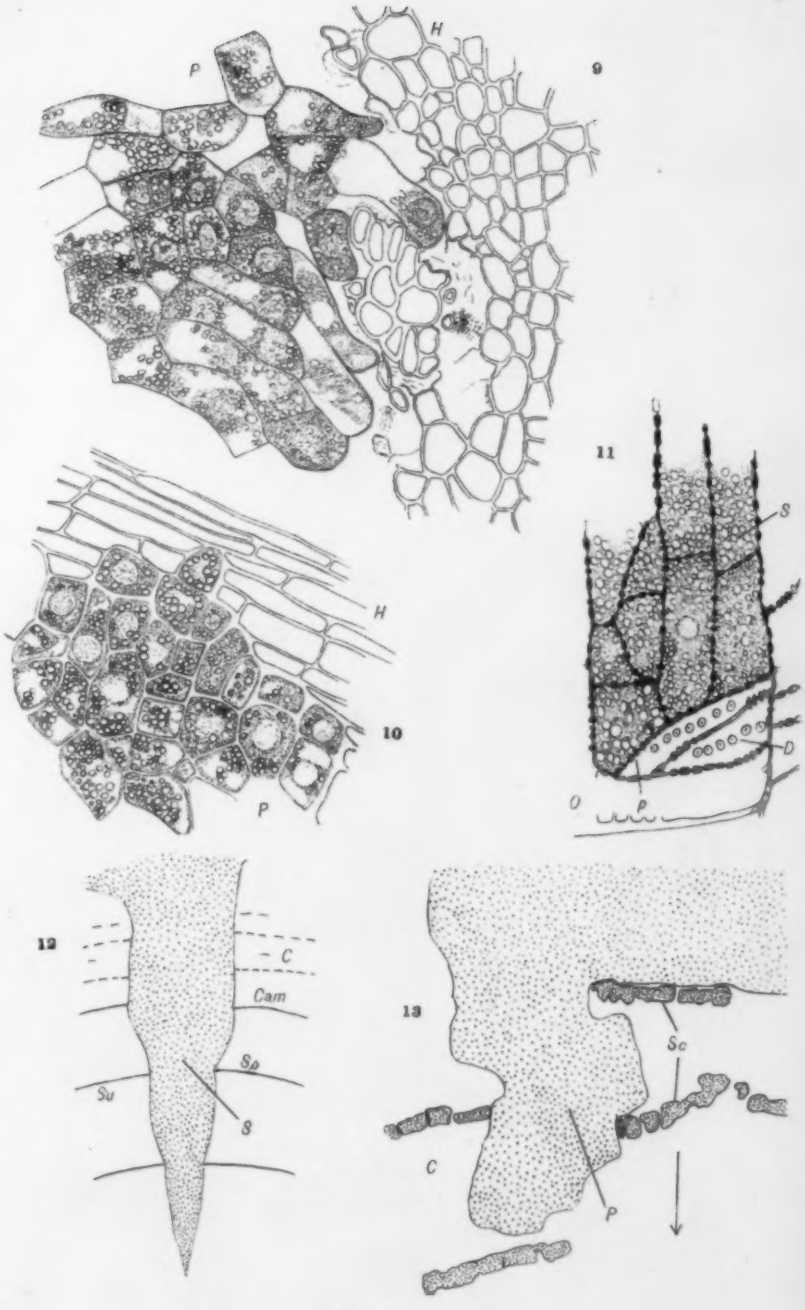


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